

***Yamaguchia toyensis* n. sp., n. gen. (Annelida, Clitellata, Lumbriculidae) from Profundal Lake Habitat in Japan**

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ABSTRACT—*Yamaguchia toyensis* n. sp., n. gen. is described from an oligotrophic caldera lake, Lake Toya, Hokkaido, Japan. Although the taxonomic affinities are unknown, the genus differs from all other Lumbriculidae in having the combination of testes and atria in X, a single, prosoporous male funnel per atrium, and spermathecae in XI. Unlike other Japanese lakes that have thus far been surveyed, Lake Toya supports abundant populations of lumbriculids in the profundal benthos.

Key words: Annelida, Clitellata, Oligochaeta, Lumbriculidae, caldera lakes

INTRODUCTION

Many oligotrophic caldera lakes are distributed among the Japanese islands. In general, the fauna of these lakes is poorly known, although in some surveys, unidentified oligochaetes are a dominant component of the profundal zoobenthos (Miyadi, 1932a, 1932b; Kitagawa, 1974, 1975a, 1975b). Although the Japanese lumbriculid fauna has received considerable study (Yamaguchi, 1936, 1937a, 1937b, 1953), members of the family have rarely been collected from profundal lake habitats in Japan. Recent collections from the profundal benthos of Lake Toya, a caldera lake in Hokkaido, Japan, indicate an unusual fauna, with abundant lumbriculids. One of these collections included several specimens of a small lumbriculid that is not clearly associated with any existing genus; that species is described in the present paper.

METHODS AND SITE DESCRIPTION

Lake Toya is a large caldera lake in the southwestern part of Hokkaido, Japan (42°36' N, 140°51'E). The surface area is 70.4 km², and the average and maximum depths are 116.3 and 179.0 m, respectively. The lake water is oligotrophic: annual average concentrations of total phosphorus, total nitrogen, chlorophyll a, and chemical oxygen demand at the lake surface are 3, 150, 0.3, and 600 µg l⁻¹, respectively (Hokkaido Research Institute for Environmental Pollution, 1990). Lake Toya is protected as part of the Shikotsu-Toya National Park. Although the lake basin supports eight thousand permanent residents and three million sightseers per year, the lake water remains oligotrophic. From 1965 to 1972

the lake received waste water from a sulfur mine, which decreased the surface pH from 7 to 5. The pH has recovered to 6.8 since the cessation of mining in 1972 (Kudo and Matsunaga, 1986). Temperature in profundal waters is approximately 4°C, and dissolved oxygen does not decrease below 80–90% saturation at any time of year (Imada, 2000). Lake Toya has been influenced by the activity of surrounding volcanoes, including recent eruptions in 1977 and 2000. However, the effects of these events on bottom communities have not been studied. Miyadi (1932a) and Kitagawa (1975a) recorded the presence of oligochaetes in the lake, but did not study their specific composition.

All specimens used in the present study were collected from profundal habitat in Lake Toya, on a single date, 12 June, 1984. Collections were made with an Ekman-Birge bottom sampler (base 225 mm), from depths ranging from 66–82 m. Bottom sediments were mostly fine mud, colored brownish at the surface, with some pumice stones.

Worms were preserved with 10% formalin solution. Sagittally sectioned specimens were cut at 7 µm increments, and transverse sections were made at 10 µm. Sections were stained in hematoxylin and eosin. Other specimens were slide mounted in Kleermount™, either as whole worms or longitudinal dissections. Body width of specimens was measured using a dissecting microscope prior to mounting on slides; all other measurements were made from slide-mounted worms, using a compound microscope.

Specimens of two potentially-related species were also examined. Supplemental observations of *Hrabea ogumai* Yamaguchi, 1936 were based on two new specimens, plus a series of photographs taken by R. Brinkhurst of sections of a type specimen. Specimens of *Kincaidiana freidris* Cook, 1965 were collected by S. Fend from several sites in western North America, and compared with the original description and that of Cook (1971).

In this description, segments are designated by Roman numerals; septa are indicated by Arabic numbers of the adjacent segments, as "4/5". Specimens from the type series have been deposited in the Division of Biological Science, Graduate School of Science, Hokkaido University (ZIHU), Japan, and the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., U.S.A.

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RESULTS

***Yamaguchia* n. gen.**

Type species: *Yamaguchia toyensis* n. sp. (monotypic).

Diagnosis: Small worms with a conical prostomium. Body wall unpigmented and bearing secondary annuli. Posterior lateral blood vessels absent. Nephridia present in VII, XIII, and some posterior segments. Testes paired in X. One pair of ovaries in XI. One pair of flattened, club-shaped atria in X, each with one short vas deferens, serving funnel on 10/11. Vasa deferentia do not penetrate septum into the post-

atrial segment. Male pores on small papillae, posterior to ventral chaetae on X. Spermathecae paired, with narrow ducts and irregular, sacciform ampullae. Spermathecal pores posterior to chaetae in XI, but medial to ventral chaetal lines; oblique muscles connect spermathecal pores to dorsolateral body wall.

***Yamaguchia toyensis* n. sp. (Figs. 1–3)**

Holotype: ZIHU 3082. A whole-mounted specimen, stained with hematoxylin.

Paratypes: All from the type locality. ZIHU 3083–3087.

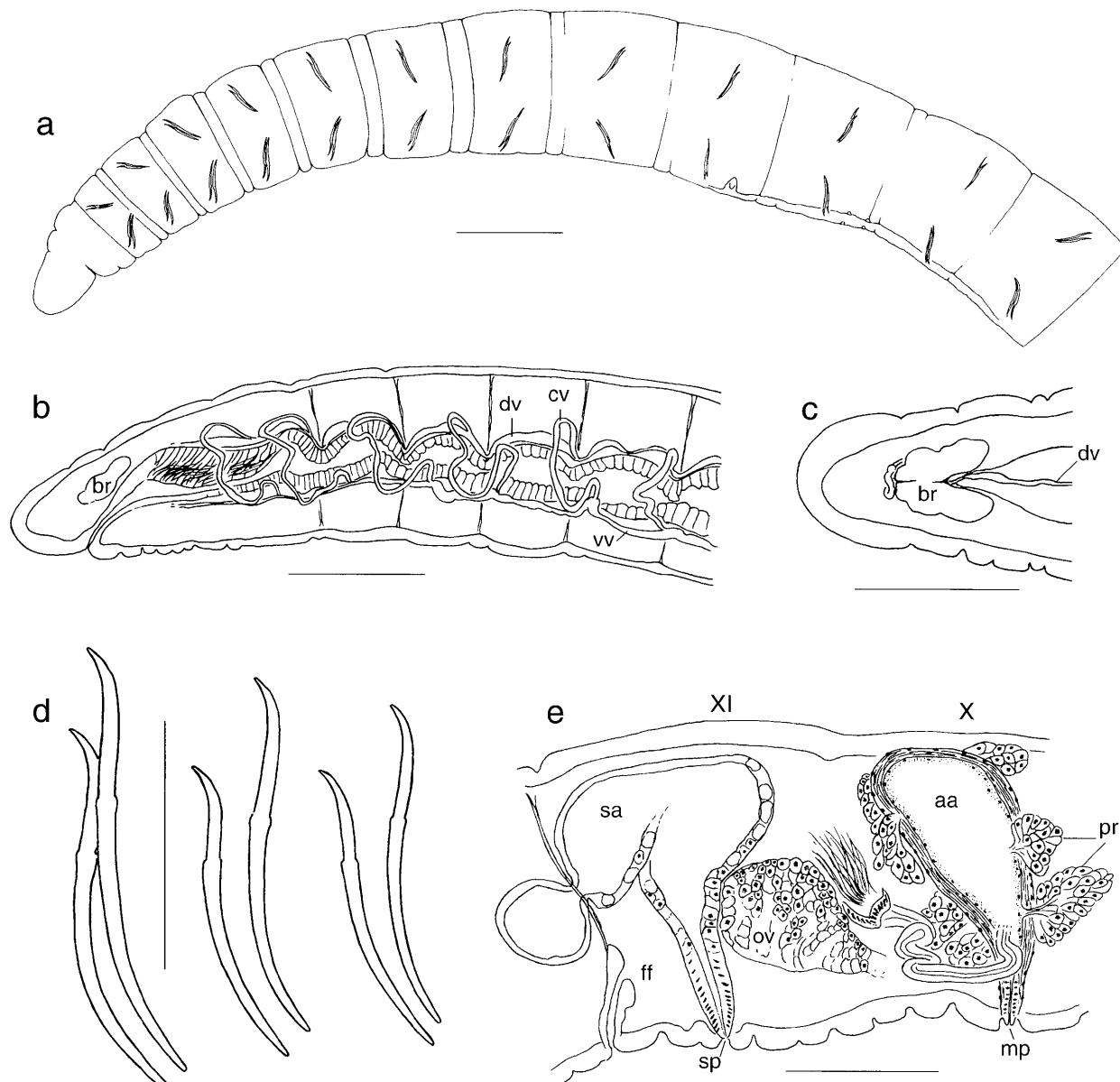


Fig. 1. *Yamaguchia toyensis*. (a–b) Lateral view of anterior segments from cleared whole mounts: external characters, segments I–XIII (a); internal characters in I–VIII (b). (c) Dorsal view of segments I–II, from a cleared whole mount. (d) Representative chaetal pairs: from left to right, preclitellar, mid-body, and posterior segments. (e) Lateral view of reproductive organs in segments X–XI, reconstructed from sagittal sections. Scale bars: (a–c), 200 μ m; (d), 50 μ m; (e), 100 μ m. Abbreviations for all illustrations: aa, atrial ampulla; br, brain; cv, lateral connective blood vessel; dv, dorsal blood vessel; ff, female funnel; gu, gut; mf, male funnel; mp, male pore; mu, muscle; pr, prostate gland; sa, spermathecal ampulla; sd, spermathecal duct; vn, ventral nerve cord; vv, ventral blood vessel

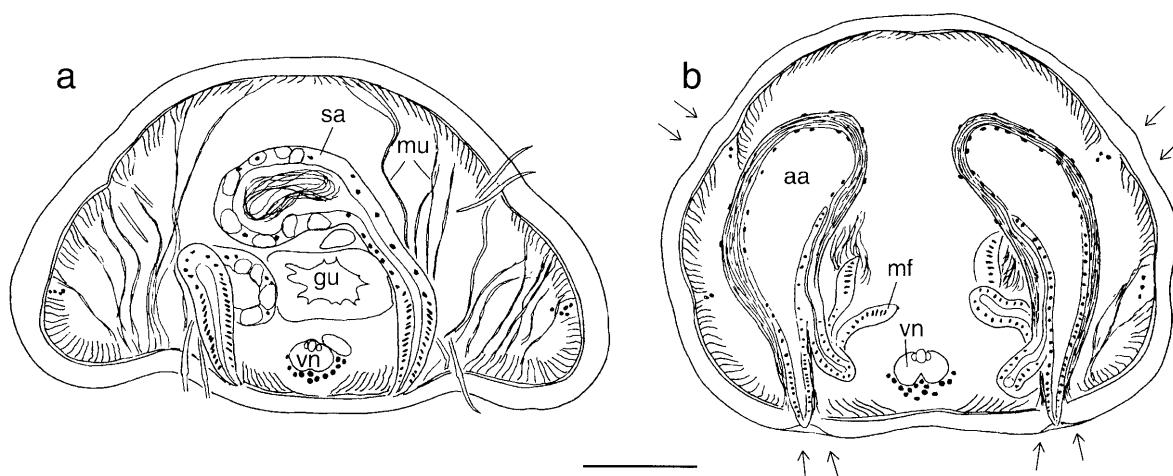


Fig. 2. *Yamaguchia toyensis*. (a) Transverse view of segment XI, showing spermathecae, reconstructed from sections. (b) Transverse view of segment X, showing atria and male pores, reconstructed from sections. Arrows show the positions of chaetae in X. Scale bar: 70 μ m

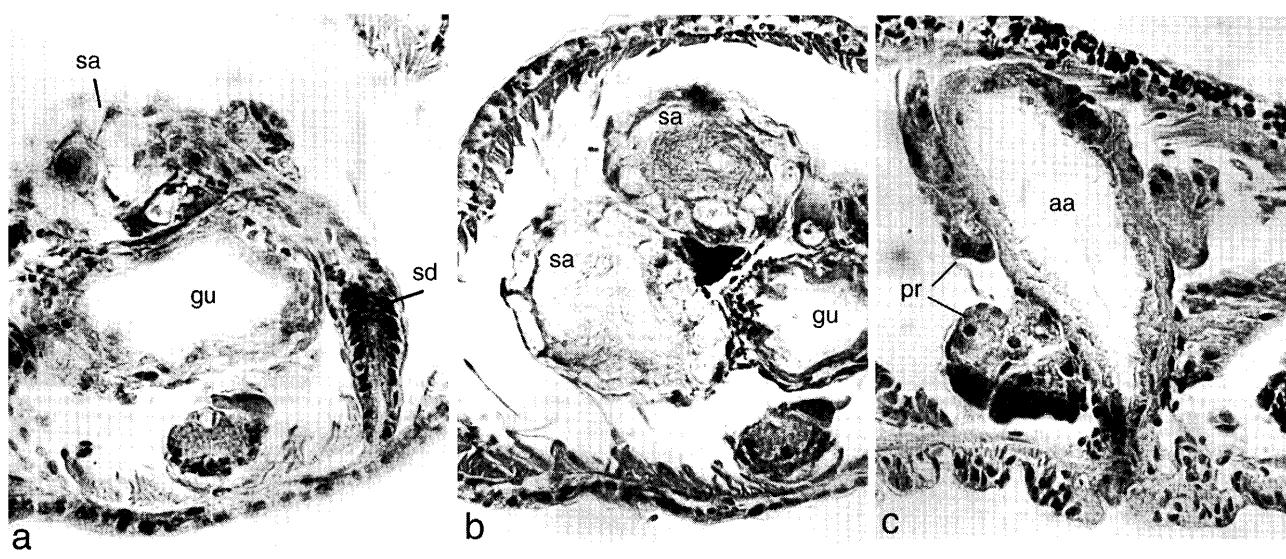


Fig. 3. *Yamaguchia toyensis*. (a) Transverse section in XI, showing a spermathecal duct. (b) Transverse section in XII, showing spermathecal ampullae. (c) Sagittal section in X, showing atrium and male pore. Scale bars: 100 μ m

Two sectioned specimens; one sagittal and one transverse, stained with hematoxylin and eosin. One longitudinally dissected specimen, stained in hematoxylin and slide mounted. Two whole-mounted specimens, stained in hematoxylin or carmine. USNM 1023105-1023109. Two sectioned specimens, one longitudinally dissected specimen, and two whole-mounted specimens.

Type Locality: Japan, Hokkaido. Lake Toya, profundal habitat (66–82 m in depth). Collected by A. Ohtaka. 12.VI.1984.

Etymology: Named for Professor Hideji Yamaguchi, who made many important contributions to the understanding of Japanese oligochaetes.

Description: Small worms, length of preserved specimens 7–11 mm, width in X 280–350 μ m. Prostomium conical, 100–120 μ m long (Fig. 1a). Chaetae closely paired in

approximately equidistant bundles, simple-pointed and sigmoid (Fig. 1d); those in preclitellar segments (II to ca. VIII) oriented anteriorly, those posterior to about VIII oriented posteriorly (Fig. 1a). Nodus distal to midpoint, about 0.35–0.3 of chaetal length from tip in anterior segments; may be slightly nearer the midpoint in posterior segments. Chaetae as short as 40 μ m in II; maximum length 67–92 μ m in segments near the clitellum; 60–70 μ m in posterior segments. Male pores paired in X, near septum 10/11, on ventral chaetal lines (Fig. 2b). Spermathecal pores paired in XI, near 11/12, slightly inside chaetal lines (Fig. 2a). Female pores indistinct on chaetal lines at 11/12. Most of body nearly round to slightly triangular in cross section, but usually dorsoventrally compressed and/or ventrally concave in XI (Fig. 2a), and sometimes in posterior segments as far as XIV. In some specimens the body wall is longitudinally indented at

the chaetal and lateral lines, and the longitudinal muscle layer is weakly separated into bands. Clitellum X-XIII, often ending in mid-XIII.

Epidermis 10–12 μm thick in anterior segments, but 24–30 μm in the prostomium. Clitellum as much as 30 μm thick, with distinctly glandular cells in fully-mature worms. Dorsal pharyngeal wall distinctly thickened in II and III; pharynx extending into IV (Fig. 1b). Pharyngeal glands in IV–VI or VII. Septa weakly developed in anterior segments. Brain in I, deeply lobed posteriorly (Fig. 1c).

One pair of lateral, dorso-ventral connective vessels near posterior septum of most or all segments from III to IX. Connective vessels rather short and not branched or strongly convoluted; they join dorsal vessel near posterior end of segment, then join ventral vessel in the following segment (Fig. 1b). No obvious lateral vessels in posterior segments. A blood vessel, probably one of the anterior connectives, loops into the sperm sacs to near their ventral ends. Dorsal vessel mostly in close contact with perivisceral sinus, but separate in clitellar region. Ventral vessel divided in segments anterior to VII. Perivisceral sinus usually weakly developed, beginning as far forward as IX in some specimens, but more strongly developed in middle segments (starting about XIV). Chloragogen weakly developed, mostly associated with dorsal blood vessel, usually beginning in VIII.

Usually a nephridium (or a pair) in VII, each with a small funnel; an irregular, granular, postseptal mass; a simple ectal duct to a nephropore just anterior to the ventral chaetae; and a posterior tubule, usually forming a dorsal loop extending to near the dorsal blood vessel, then running midventrally for one or two segments posteriorly. Ectal duct slightly expanded at nephropore, but without a distinct ampulla. Similar nephridia usually paired in XIII, then irregularly occurring in a few posterior segments; posterior tubules may extend posteriorly through two or more segments.

Ovaries paired in XI. Usually one egg sac developed, with mature eggs in one or two segments behind one of the sperm sacs. Female funnels about 80 μm long, on 11/12.

A single pair of testes in X, with two sperm sacs extending posteriorly as far as XVII. A single pair of male funnels on 10/11, directed posteriorly and extending back into sperm sac (Fig. 1e); maximum funnel width about 100 μm . Vasa deferentia do not penetrate septum into the post-atrial segment. Vasa deferentia short, 90–130 μm long; diameter 10–19 μm ; joining inner side of atria at about the ectal 1/4. In one specimen, vasa appear to run between atrial lining and outer muscle layer, entering lumen near the midpoint (Fig. 2b). In other specimens, the atrial lining is indistinct (Fig. 3c), and vasa appear to enter lumen directly. Atria one pair, entirely in X; laterally compressed, broadly club-shaped (Fig. 1e), 180–250 μm long and 65–105 μm wide at the widest point; usually extending to near the dorsum and somewhat curving over the gut (Fig. 2b). Short ectal duct of atrium about 12–20 μm wide. Atrial muscle a single layer, 6–10 μm entally, thinner ectally; with fibers arranged in an irregularly circular (transverse) direction. The wide lumen is

lined with an irregular layer of ciliated, granular epithelium having indistinct cell boundaries (Figs. 1e, 3c). Multicellular prostate glands in a few (up to 10) irregular bundles, up to 60 μm long, arranged along anterior and posterior sides of atria (Figs. 1e, 3c), but absent from lateral sides (Fig. 2b). Prostate bundles on short stalks, which penetrate the atrial muscle and join the layer of atrial lining cells. Male pore on a small, conical papilla 5–12 μm long. Papilla in a small depression not associated with obvious glands, or muscles, but sometimes within a ring of slightly thickened epidermal cells (Fig. 3c).

Spermathecae one pair, with narrow ectal ducts in XI. Irregular ampullae begin in XI, usually extending into XII or XIII (Fig. 1e). Spermathecal ducts 80–130 μm long; maximum width 18–26 μm , slightly narrowed ectally. Ducts with columnar epithelium in the ectal half, and cuboidal epithelium entally (Fig. 3a). Lining cells of ampullae irregular and often vacuolar, sperm in a loose bundle (Fig. 3b). Ampullae constricted at septa; greatest diameter 70–130 μm , in XI, or more commonly in XII. In the posterior part of XI and sometimes to a lesser extent in XII, many long, oblique muscles attach laterally to the spermathecal pores, near the ventral chaetal lines, and dorsally, near the dorsal chaetal lines (Fig. 2a).

Remarks: Most specimens were complete, and appeared fully mature. Mature specimens had a well-developed clitellum, sperm in the spermathecae, and mature eggs in the egg sacs. The material appeared to be in good histological condition.

The extensive musculature surrounding the spermathecal pores appears to raise the entire floor of segment XI, and to some extent XII. Although the resulting concavity is quite shallow, it could form a chamber to facilitate sperm exchange. Flattening of the spermathecal segment is unusual, but similar musculature is associated with the male pores in other lumbriculids (e.g. *Tatriella* Hrabě, 1936 and *Secubelmis* Fend and Gustafson, 2001), and dorsoventral muscles flatten the ventral side of the atrial segment in other oligochaete families. Dorsoventral musculature apparently serves to retract the evversible penes of some lumbriculids (e.g., *Rhynchelmis rostrata* [Eisen, 1888] and *Eclipidrilus palustris* [Smith, 1900]), and the spermathecal porophores of *Eremidrilus felini* Fend and Rodriguez, 2003, but the copulatory organs of *Y. toyensis* are weakly developed in comparison. The laterally compressed atria and the restriction of the prostates to the anterior and posterior sides of the *Y. toyensis* atria are also unusual, but these characters could simply be a consequence of packing large organs into a small worm. Laterally compressed atria also have been reported for *Trichodrilus hrabei* Cook, 1967.

The male pores are rather consistent in size and form, and thus do not appear to vary much with state of contraction. In some whole-mounted specimens there appears to be a slight change in texture of the epidermis in a small ring around the male pore, and in some there is a small accumulation of possibly glandular cells. The small papillae, which could be described as "penes", appear to be simple

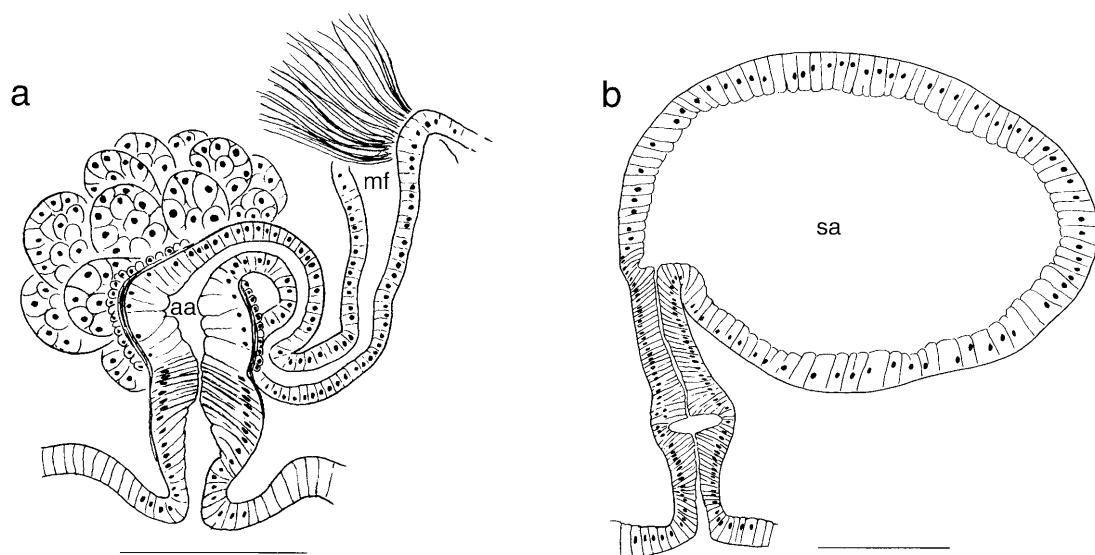


Fig. 4. *Hrabea ogumai*. Lateral views of reproductive organs, from dissected specimens. (a) Atrium, vas deferens and male funnel. (b) Spermatheca. Scale bar: 100 μ m

extensions of the atrial duct. The spermathecal pores are also very simple, other than the lateral musculature; their somewhat median position, although unusual, occurs in other lumbriculid species.

Hrabea ogumai Yamaguchi, 1936 (Fig. 4)

Material Examined: Toma Cave, Kamikawa, Hokkaido, Japan, collected by A. Ohtaka 29.VIII.1985. Two sagittally dissected specimens, stained in borax carmine and slide mounted.

Remarks: The original description (Yamaguchi, 1936) included photographs of atrial sections, but did not describe their morphology in detail. The short atria are divided into an ectal duct and an ental ampulla (Fig. 4a). The ectal part of the duct appears to be a broad epidermal infolding, similar to the penial sacs of other Lumbriculidae. More entally, the epithelial cells become more tightly packed and elongate, and the lumen is constricted (Plate V, Fig. 7 in Yamaguchi, 1936). The ampulla is about as wide as long, with an irregular lumen; a distinct ectal muscle layer, about 5 μ m thick, surrounds a thick epithelium with basal nuclei. A dense layer of pyriform prostate glands, each containing several cells, covers the atrial ampulla. The vasa deferentia are very short and thick (diameter 25–34 μ m in the dissected specimens); a single vas deferens joins each atrium at the ental end. The spermathecal pores are within a shallow concavity, but are not associated with extensive musculature. The spermathecal ducts have a distinct median expansion in the two dissected specimens (Fig. 4b); part of a similar expansion may be illustrated in the original description (Plate V, Fig. 4 in Yamaguchi, 1936). One additional character not mentioned in the original description is that the female pores are slightly posterior to septum in segment XI, in the groove forming the anterior secondary annulus. In both of the dissected specimens, the female funnels extend through septum 10/11, and

thus would be considered plesioporous (Brinkhurst 1989).

DISCUSSION

Taxonomy

The most comprehensive taxonomic treatments of lumbriculid genera have been the review by Cook (1971) and the phylogenetic analysis (based on characters in published descriptions) by Brinkhurst (1989). However, our subsequent attempts at phylogenetic analyses of the Lumbriculidae, using those characters with some corrections and additions of newly-described taxa, have been inconclusive, suggesting that a rigorous phylogenetic argument is not possible at this time. A revision of the family would require an extensive review of the characters, and is beyond the scope of the present study, particularly in view of current work in progress using molecular and ultrastructural characters (Erséus and Källersjö, 2004; Dr. M. Ferraguti, University of Milan, personal communication). Therefore we take the approach of relating the new species to similar taxa in terms of (1) the Brinkhurst (1989) analysis, (2) the generic definitions presented in Cook (1971), and (3) overall morphological similarity to other lumbriculids.

Using the character definitions from the Brinkhurst (1989) analysis, character states of the new species and the three most similar taxa are given below. The position of the female pores (Character 16) in *Hrabea* was indicated as "unknown", but based on the new specimens; they are now coded as plesioporous. In the original matrix, Character 19 was erroneously given the value 1 for *K. freidris* (posterior lateral blood vessels present). Cook (1971) described that species as lacking these blood vessels, and this was verified by our observations of many new specimens.

00000 11030 01010 11000 011000 *Trichodrilus cernosvitovi* group

00100 11030 10010 13000 111000 *Kincaidiana freidris*
 00100 11010 00000 01000 111000 *Hrabea ogumai*
 00000 13020 01000 11000 001000 ancestral lumbriculid (hypothetical)
 00100 11030 00000 11000 111000 *Yamaguchia toyensis*

According to the matrix, the closest match to the new species is the monotypic *Hrabea ogumai* Yamaguchi, 1936, which differs mainly in having spermathecae in the pre-atrial segment (Character 9). Brinkhurst's (1989) parsimony analysis suggested that a trend in lumbriculid phylogeny was from semiprosoporous (two vasa deferentia per atrium, serving testes in the atrial and pre-atrial segments) to prosoporous (a single vas deferens per atrium, serving testes only in the atrial segment). This would involve Characters 3 (0–1: testes present/absent in pre-atrial segments) and 12 (1–0: each atrium with 1/2 vasa deferentia), and these changes could thus be synapomorphies for a group containing the new species plus *H. ogumai*. Character 21 (0–1: posterior vas deferens penetrates/does not penetrate the post-atrial septum) provides another possible synapomorphy, but the derived state also occurs in several other genera. Most other characters associating the new species with *H. ogumai* (e.g., lack of penes and lateral blood vessels, Characters 14 and 19) appear to be plesiomorphic in the Brinkhurst analysis. Although Character 22 (presence of atria) is considered an apomorphy with respect to the hypothetical ancestor, "atria present" is the character state for all lumbriculid genera. The position of the female pores (Character 16) was indicated as "unknown" in the original Brinkhurst matrix, but based on the new specimens, they are now coded as plesioporous.

Like the new species, *H. ogumai* has short, prosoporous male ducts, and is endemic to Japan. However, additional characters not included in the above matrix do not provide strong evidence for relating the two species. The atria of *H. ogumai* have a thick, complex ectal duct, in contrast to the simple papilla of *Y. toyensis*. The very small atrial ampulla of *H. ogumai* contrasts with the club-shaped ampulla of *Y. toyensis*, and suggests the possibility that Character 11 (atria pear-shaped/elongate) also should be reconsidered.

Cook (1971) defined genera in the family Lumbriculidae primarily by the numbers and relative positions of the genital organs. According to those definitions, the new species is closest to *Kincaidiana freidris*, which differs in having the gonads shifted forward by two segments from the X–XIII regarded by Brinkhurst (1989) as plesiomorphic within the Lumbriculidae (Character 17). *Kincaidiana* is a Nearctic genus containing two species having little morphological similarity, and Brinkhurst's (1989) analysis suggests that it is not monophyletic. As in the case of *Hrabea*, the prosoporous condition could be considered a synapomorphy for *K. freidris* and the new species, *Y. toyensis*. Both species have a single pair of spermathecae with long ectal ducts and elongate ampullae, and short vasa deferentia that enter the atrium in the ectal portion. However, in addition to the forward shift in gonadal segments, *K. freidris* differs from *Y.*

toyensis in several characters: large penes (Character 14), longer, petiolate atria (Character 11), and spermathecal pores having distinct vestibules, but without extensive musculature (Cook, 1971).

Two additional lumbriculid genera, *Lumbriculus* Grube, 1844 and *Trichodrilus* Claparède, 1862, include members with spermathecae in the first post-atrial segment. *Lumbriculus* is unlikely to be closely related; although it is quite variable, it usually has two or more spermathecal segments beginning in the second post-atrial segment, with spermathecal pores dorsal to the ventral chaetal line. In addition, *Lumbriculus* has branched lateral blood vessels, characteristic penes, and sometimes additional atrial, testicular, or ovarian segments. In other genera with post-atrial spermathecae (*Lamprodrilus* Michaelsen, 1901; *Lamprortus* Rodriguez, 1994), the spermathecae always begin in the second post-atrial segment, and, as in the case of *Lumbriculus*, none of the species bears much resemblance to *Y. toyensis*.

The new species could be associated with some *Trichodrilus*, particularly those referred to by Brinkhurst (1989) as the "cernosvitovi group", which have spermathecae only in the first post-atrial segment, and lack lateral blood vessels in posterior segments. The primary differences are the semiprosoporous atria (the plesiomorphic state for Characters 3 and 12), and 21. Character 21 is coded "0" for *Trichodrilus* because the posterior vasa deferentia penetrate the posterior septum in most species; nevertheless, the alternate condition occurs in some species. The implied loss of the anterior pair of testes and male funnels in *Yamaguchia* is not unlikely, as it occurs within other lumbriculid genera (*Rhynchelmis*, *Eclipidrilus*, *Lumbriculus*, and *Phagodrilus* McKey-Fender and Fender, 1988). However, in some of these genera, this process may be inferred from the occurrence of "intermediates" with reduced or vestigial anterior vasa deferentia. No such reduction of anterior testes or vasa deferentia has been described in any *Trichodrilus* species.

In summary, although *Y. toyensis* lacks novel characters that would indicate unambiguous apomorphies, the combination of prosoporous male ducts in X and a single pair of spermathecae in XI is not found in any of the previously-described genera. Inclusion in *Hrabea* would be contrary to traditional generic definitions (Cook, 1971), as it would associate species having spermathecae in post-atrial versus pre-atrial segments; the only genus in which this is accepted is *Styloscolex* Michaelsen, 1901. However, the three *Styloscolex* species having post-atrial spermathecae instead of (or in addition to) the usual pre-atrial ones can be associated with congeners by several synapomorphies, including elongate penes, a forward shift of the reproductive segments, and ovaries two segments posterior to the testes (Timm, 1994).

Inclusion of *Y. toyensis* within *Kincaidiana* would add further confusion to an already paraphyletic genus, and would associate species having very different copulatory structures. Also, a distributional expansion of *Kincaidiana* into the Palearctic should be justified by more convincing

synapomorphies. Inclusion in *Trichodrilus* would require further expanding the definition of that genus, which is already large and sometimes weakly differentiated from other genera (Giani and Rodriguez, 1994). This change would probably also require the inclusion of *Kincaidiana freidris* in *Trichodrilus*. In the absence of synapomorphies that are complex, unique, or otherwise compelling, it seems that the most conservative approach is to designate a new genus.

Ecological notes

Lumbriculids are an important component of some northern oligotrophic lakes (Martin, 1996), but the family has rarely been reported from the mostly eutrophic lakes that have been surveyed in Japan (Ohtaka and Kikuchi, 1997). Although an unidentified lumbriculid was once recorded from profundal habitat in formerly oligotrophic Lake Biwa (Stephenson, 1917), that lake has suffered from eutrophication in the last 30 years. Recent surveys of the Lake Biwa profundal zone have not detected lumbriculids, although *Lumbriculus* species have been collected in littoral habitats (Nishino *et al.*, 1999). A report of *Lumbriculus variegatus* (Müller, 1774) from oligotrophic Lake Towada (Ohtaka, 2001) is the only other published record of the family in Japanese profundal lake habitat. In contrast, lumbriculid worms are abundant in the profundal benthos of Lake Toya. Immature and partially-mature specimens that are probably attributable to *Styloscolex japonicus* Yamaguchi, 1937 were the most abundant oligochaetes on three collection dates in May and June, 1984, as well as in a recent survey completed in 2001; other oligochaetes in those collections included haplotaxids and both rhyacodriline and tubificine tubificids (Ohtaka, unpublished).

Caldera lakes in Japan generally originated during or subsequent to the most recent glacial maximum (Saijo and Sakaguchi, 1978); as a consequence, Ohtaka (2001) attributed the benthic fauna of another oligotrophic caldera, Lake Towada, to colonization from lotic habitats in the surrounding watershed. Lumbriculids also are often a major component of the groundwater biota (Giani *et al.*, 2001), and the dominant Lake Toya species, *S. japonicus*, is typically found in groundwater or springs in Hokkaido (Yamaguchi, 1937b; Ohtaka unpublished data). Although it is possible that the new species is derived from groundwater populations, springs have not been detected on the floor of Lake Toya.

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